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Research Article

Genome-wide target enriched viral sequencing reveals extensive 'hidden' salmonid alphavirus diversity in farmed and wild fish populations

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Abstract

Aquaculture plays a crucial role in global food and economic security, though its expansion and sustainability remain under threat from infectious diseases. Salmonid alphavirus (SAV, *Togaviridae*), the causative agent of pancreas disease and sleeping disease, is responsible for large negative impacts in salmonid aquaculture. Few studies have characterised this virus at a genome-wide level, and the extent of intrahost SAV genetic diversity remains largely unexplored. Pooling tissues from multiple infected animals is a standard method of sampling for molecular diagnostics of pathogens in aquaculture; however the impacts of pooling on detection of viral diversity remain poorly understood. Here we applied a sequence capture strategy to obtain SAV genomes at high coverage from infected fish using both pooled and individual samples. We compared the genetic diversity of SAV in farmed Atlantic salmon and rainbow trout, in addition to two wild flatfish species, sampled from multiple regions in Scottish and Irish waters. Mixed subtype infections were present in three of the four species studied, and in both farmed and wild samples. This involved pairs of SAV subtypes known to previously exist in the sampled geographical locations. Evidence of subtype-level SAV co-infections were also shown in individual fish (i.e. not pooled), including wild fish such as dab. Our findings confirm the circulation of multiple SAV subtypes on the same fish farm and abundant within-subtype genetic diversity in all studied samples. Further, the pooling of samples from different fish clearly underestimates the genetic diversity characterizing infections, and likely limits the power to detect the transmission of novel viral genotypes into different geographic regions or fish farms. We conclude that SAV transmission and evolutionary dynamics are more complex than recognized currently, and should be routinely characterized at a genome-wide level to capture the true diversity associated with disease outbreaks, providing stronger information for decision-making on disease control.

1. Introduction

The rapid evolutionary rate of RNA viruses leads to high levels of genetic diversity and the potential for co-existence of multiple strains in host populations, including within single hosts (Duffy et al., 2008; Sanjuán et al., 2010). Such diversity poses challenges to both human health and agricultural systems, as the effectiveness of disease control relies on knowledge of both viral diversity and evolutionary dynamics (Acosta-Leal et al., 2011; García-Arenal and McDonald, 2003; Grenfell et al., 2004). Aquaculture, as the fastest growing food production industry (FAO, 2016), plays an increasingly important role in global food and economic security (Jennings et al., 2016). However, viral disease remains a major threat to the sustainability and expansion of this sector, due to a lack of effective therapeutics and vaccines (Garver et al., 2005; Karlsen et al., 2012; Munang'andu et al., 2012) and limited understanding of disease transmission between farmed populations and wild reservoir fish (Bruno et al., 2014; Ruane et al., 2018; Snow et al., 2010).

Molecular characterization of pathogens plays an important role during investigations of viral disease outbreaks on fish farms, helping to understand the transmission of pathogens between farms, and contributing to improvement of disease control measures to further limit pathogen transmission. Sanger sequencing of up to a few (2-3 on average) candidate/marker genes is often applied to characterize the disease agent (Holopainen et al., 2017; Matejusova et al., 2013; Nishizawa et al., 2006) and this method is accurate and well suited to low-throughput applications aiming to reveal the dominant viral strain(s). Second generation high-throughput sequencing (e.g. Illumina, Roche 454, Ion Torrent etc.) is now well established for genome-wide investigations of animal viruses (Bodewes et al., 2013; Ferretti et al., 2018; Pfaff et al., 2018) and, like Sanger, provides highly accurate data. Recent studies have demonstrated the potential of such platforms to reveal intrahost diversity of fish viral pathogens, e.g. of viral hemorrhagic septicaemia virus (VHSV) (Schönherz et al., 2016) and Cyprinid herpesvirus 3

(Hammoumi et al., 2016). Third generation Nanopore sequencing has recently been used for rapid genome-wide analysis of fish RNA viruses (Gallagher et al., 2018), but this platform still suffers from higher error rates compared to Sanger and Illumina platforms, making finer-scale investigations of viral genetic diversity more challenging.

Understanding the genetic diversity of natural viral infections is essential, as different viral strains may be associated with unique pathological outcomes, demanding alternative control strategies. For example, while infectious salmon anaemia virus (ISAV) typically causes high mortality rates in Atlantic salmon, a specific ISAV strain (HPR0) is non-pathogenic (Nylund et al., 2006). However, as co-infections with both pathogenic and non-pathogenic ISAV strains have been reported (Kibenge et al., 2009; Kulshreshtha et al., 2010), and ISAV HPR0 has been shown to mutate into a pathogenic form (Christiansen et al., 2017), the ability to accurately capture all viral forms within each host is necessary for effective decisions on disease control. Similarly, different strains of VHSV have distinct outcomes for pathogenicity in salmonids (Dale et al., 2009; Skall et al., 2004) and the introduction of the exotic VHSV genotype IV into Europe could have devastating consequences (Lumsden et al., 2007). Thus, the ability to detect co-infecting viral strains is central to viral epidemiological studies and the control of viral disease outbreaks.

In this study, we used a capture-based approach to enrich the whole genome of target viruses and used it to characterize genetic diversity of salmonid alphavirus (SAV, *Togaviridae*), a single-strand positive-sense RNA virus. This virus was recently added to the World Organisation for Animal Health ('OIE') list as a notifiable disease agent (OIE, 2019). SAV causes pancreas disease (PD) in Atlantic salmon *Salmo salar* and sleeping disease (SD) in rainbow trout *Oncorhynchus mykiss*, resulting in significant mortality, reduced growth and poor flesh quality (Aunsmo et al., 2010). Six SAV subtypes (SAV1-6) are widely recognized (Fringuelli et al., 2008) that are loosely geographically structured across Europe, with Scotland

reporting cases of SAV1, 2, 4 and 5, Ireland SAV1, 4 and 6 (Graham et al., 2012), and Norway SAV2 and 3 (Hjortaas et al., 2013; Hodneland et al., 2005). SAV has also been detected in wild species including flatfish (Bruno et al., 2014; Snow et al., 2010) and Ballan wrasse *Labrus bergylta* (Ruane et al., 2018). While one past study provided evidence for complex population structure in SAV3 (Petterson et al., 2013), including the presence of non-random deletion variants in natural infections, epidemiological studies of SAV have been limited to the subtype-level; omitting intrahost variation. Considering that different SAV subtypes are known to have unique pathogenicity (e.g. infections with SAV1 and SAV3 show the most pronounced histopathological changes) (Graham et al., 2011), and the recent addition of SAV to the OIE notifiable list, gaining a deeper understanding of SAV genetic diversity and population structure is of broader interest to both the aquaculture and academic industries.

We thus performed a genome-wide analysis of SAV diversity within infected tissues from farmed salmonid and wild flatfish samples from several locations, representing both single hosts and pools of different fish. We reveal extensive genetic diversity on several levels, including SAV subtype co-infections in single wild hosts, the presence of multiple SAV subtypes at the farm level, and extensive within-subtype SAV diversity in all samples. Our findings have implications for sampling strategies of epidemiological and transmission studies and disease management where strain-level information is relevant.

2. Materials and methods

2.1. *Sample Preparation*

Tissue homogenate or RNA from eighteen heart tissue samples from either individual fish or pools (n=5 fish) with natural SAV infections were obtained from Marine Scotland Science or Marine Institute Ireland (Table 1). Irish flatfish from Marine Institute Ireland were previously published (McCleary et al., 2014). Total RNA was extracted using a phenol-chloroform method and RNA integrity was assessed by agarose gel electrophoresis. Single-strand (ss)-cDNA was

synthesized using Superscript III reverse transcriptase (Invitrogen) and cleaned by AMPure XP bead purification (Beckman Coulter). Ss-cDNA was converted to double-strand (ds)-cDNA using NEBNext Ultra II Non-directional RNA Second Strand Synthesis Module (New England Biolabs) following the manufacturer's instructions. Ds-cDNA concentration was determined using a Qubit system with a ds-DNA HS Assay kit (ThermoFisher). Relative viral load was estimated using qPCR (Table 1), employing a primer pair designed in a region of the SAV genome conserved across all subtypes: 5' - TGC CCG ACA GAG CAC CTT - 3' (sense) and 5' - CTC GGC GAC CTG GAA CTT GAT - 3' (antisense). 15 µl qPCR reactions were performed for each isolate including 5 ng ds-cDNA, 7.5 µl Brilliant III Ultra-fast SYBR Green (Agilent Technologies) and 500 nM sense/antisense primers. Cycling conditions were as follows: 1 cycle of 3 min at 95°C, followed by 40 cycles of 20 s at 64°C, finishing with 30 s at 55°C. The ds-cDNA samples were kept at -80ºC until library preparation for sequence capture.

2.2. *Sequence capture probe design, library preparation and sequencing*

Agilent SureSelect^{XT2} 120-mer RNA oligomer baits were generated at 4-fold tiling to cover reference genomes for SAV1 to SAV5 (where possible representing two representatives of the most phylogenetically distant clades) (accession numbers: SAV1: JX163854, AJ316244; SAV2: AJ316246, MH708652; SAV3: DQ149204, SAV4: MH708651; SAV5: MH708653, MH708650), as well as two fragments of SAV6 (EF675547, EF675499). Sequence capture library preparation and Illumina sequencing were performed by the Centre of Genomic Enabled Biology and Medicine (CGEBM) at the University of Aberdeen. 100ng of ds-cDNA from each sample was sheared using sonication, end-repaired and purified with AMPure XP beads. The pre-capture SureSelect^{XT2} reagent kit was used to ligate single i7 indexing adapters to the DNA fragments and the libraries were amplified using PCR before quality assessment on an Agilent TapeStation. Sequence capture was performed with the custom baits following the

146 manufacturer's instructions. Indexed samples were pooled together for the hybridisation step,
147 where RNA baits bound to the virus cDNA were captured using a streptavidin bead-based
148 separation. Captured libraries were amplified using PCR (12-14 cycles) and the amplified
149 library confirmed using the Agilent BioAnalyser. The pooled library was run on a single
150 NextSeq500 flowcell (2x150bp pair-end configuration) according to Illumina specifications.
151
152 2.3. *SAV genome analysis*
153 Demultiplexed FASTQ files were trimmed of sequencing adapters and poor-quality bases
154 using TrimGalore v.0.4 (min q-score of 30) (Krueger, 2015). The average cDNA fragment size
155 prior to adapter ligation was 192 bp, leaving an overlap between 2 x 150 bp paired reads. Paired
156 reads were merged into longer contigs when possible using the BBMap (Bushnell, 2016)
157 programme BBMerge (default settings). Both merged and unmerged reads were used for
158 subsequent analyses (average sequence length: 187 bp). PCR duplicates were removed using
159 DeDupe (BBMap package) with default parameters. BBSplit (BBMap package) was used to
160 align all quality controlled passed reads of each isolate to a reference of each of the six subtypes
161 (SAV1 - AJ316244; SAV2 - AJ316246; SAV3 - DQ149204; SAV4 - MH708651; SAV5 -
162 MH708653; SAV6 - MH238448). Different SAV subtypes were considered present in the
163 same sample when >50 reads mapped to locations of the reference sequence that contained
164 subtype-unique variants (e.g. as visualized in Fig. S1). The resulting bins of reads were mapped
165 to the corresponding reference genome with BWA-MEM (Li, 2013), using default settings and
166 the alignments were then processed using SAMtools v1.3.1 (Li et al., 2009). Consensus
167 sequences were generated using FreeBayes variant-calling (Garrison and Marth, 2012) and the
168 VCF manipulation package vcflib (Garrison, 2012) to produce a FASTA file for each subtype-
169 specific isolate. The percentage of the SAV genome captured in each consensus sequence was
170 calculated (Table 2) by comparison to a reference sequence of the same subtype. Proportions

171 of each subtype per sample were estimated by comparing sequencing depth of each assembly
172 across ORF2 (Fig. 1)
173
174 2.4. *Bayesian phylogenetic analysis*
175 Isolate sequences from which ≥85% of the structural polyprotein (ORF2) was assembled were
176 used for phylogenetic analysis, along with all unique published SAV ORF2 sequences (isolate
177 names given in Fig. 2). Sequence alignment (n=51 sequences) was performed using MAFFT
178 v.7 with default parameters (Katoh and Standley, 2013). The final alignment was 3,917 bp in
179 length and is provided in the Supplementary Information (Dataset S1). Prior to phylogenetic
180 analysis, the best fitting nucleotide substitution model was estimated using IQTREE v1.5.3
181 (Nguyen et al., 2015; Trifinopoulos et al., 2016). Bayesian phylogenetic analysis was
182 performed using BEAST v.2.4.4 (Bouckaert et al., 2014), employing the best fitting nucleotide
183 substitution model (general time reversible model; Tavaré, 1986, with gamma distribution of
184 among-site rate variation estimated under 4 rate categories) an uncorrelated lognormal relaxed
185 clock model (Drummond et al., 2006), a random starting tree and a Bayesian coalescent
186 constant population model (Drummond et al., 2005). The Markov Chain Monte Carlo (MCMC)
187 chain length was 200 million generations, with sampled parameters logged every 20,000
188 generations. Convergence and mixing were assessed using Tracer v.1.6 where all effective
189 sample size statistics (ESS) were >200. A maximum clade credibility tree was created using
190 TreeAnnotator (Drummond et al., 2012) after removing the first 10% of trees as burn-in, The
191 resulting tree (Fig. 2) was visualised in FigTree (http://tree.bio.ed.ac.uk/software/figtree/).
192
193 2.5. *Subtype-specific SAV genetic diversity*
194 Bins of sequence reads representing different SAV subtypes were mapped back to their
195 consensus sequence (generated as outlined above) using BWA-MEM, with alignment

196 processing performed using SAMtools. SNV detection was then performed using FreeBayes,
197 with stringent parameters to reduce type-I error: a minimum base quality of 30, a minimum
198 mapping score of 30, a minimum variant frequency of 0.05, a minimum coverage of 50 reads,
199 and a p-value of $< e^{-7}$. All SNVs were visually inspected and their effect on coding sequence
200 determined. Genomic location of each SNV from each isolate was determined, plotted in
201 reference to an SAV genome alignment (n=31) using the R package ggplot2 (Wickham, 2009),
202 and coloured by both codon effect (Fig. 4) and novelty of the SNV in question (Fig. S2).
203 Samples from which a subtype-consensus sequence could be obtained were further analysed to
204 determine the percentage of the genome which was variable (i.e. proportion of the nucleotide
205 sites which contained an SNV) (Table 3).
206
207 2.6. *Intra-subtype haplotype reconstruction and phylogenetic analysis*
208 Due to inconsistent results obtained from several haplotype reconstruction softwares,
209 haplotype reconstruction of small genomic regions (~350 bp) was performed manually using
210 visualised alignments on IGV (Thorvaldsdóttir et al., 2013). Isolates were chosen for analysis
211 based on visualisation of SNVs; only those with several SNVs each located within the
212 maximum read length (~250bp) of the next SNV were considered (samples IRE/3/12,
213 IRE/38/11, SCO/G415/09, SCO/G572/09, SCO/G573/09, and SCO/G582/07). A genomic
214 region overlapping the E3 and E2 genes was selected to maximise the number of SNVs present
215 in the samples. SNVs were considered to belong to the same haplotype if >99% of the reads
216 with one SNV also contained a second SNV, itself present in <1% of reads not containing the
217 first SNV. Haplotype sequences generated for samples IRE/3/12, IRE/38/11, SCO/G415/09,
218 SCO/G572/09, SCO/G573/09, and SCO/G582/07 were aligned against the same regions of
219 consensus SAV1 sequences recovered for other samples within the study, before a Bayesian
220 phylogenetic analyses was performed as described above.

221

222 **3. Results**

223 3.1. *Sequence capture for genome-wide SAV analysis*

224 Eighteen tissue samples from four fish species (Atlantic salmon, rainbow trout, European
225 plaice *Pleuronectes platessa* and common dab *Limanda limanda*) were used in this study
226 (Table 1). For the farmed salmonid samples, heart tissue from a representative sample of five
227 fish, pooled together at the farm level, were obtained during routine visits to fish farms on the
228 west coast of Scotland and Shetland. The pooled wild flatfish were caught on the east coast of
229 Scotland, while the individual flatfish samples were caught in Dublin bay and the Celtic sea.
230 All samples tested positive for SAV using qPCR analysis (Table 2). The samples were
231 sequenced on an Illumina NextSeq 500 following enrichment of SAV cDNA using the Agilent
232 SureSelect^{XT2} platform. The sequence capture probes covered the full genomes of SAV1-SAV5
233 genotypes and also included two partial fragments of SAV6 (Fringuelli et al. 2008).

234 In total, 136,914,992 reads (20.5Gb total DNA) were obtained that passed quality control
235 (Table 2). The proportion of SAV reads among all sequenced reads ranged from 2.9% to 91.4%
236 per sample (Table 2) and was positively correlated with viral RNA load estimates obtained by
237 qPCR (Pearson's R=0.92, p<0.001). Sequence coverage was uneven across the genome, with
238 more reads mapping to ORF2 (structural polyprotein) than ORF1 (non-structural polyprotein)
239 for SAV1, and a higher 3' coverage of each polyprotein for SAV2 (Fig. S1).

240 3.2. *Evidence for co-presence of different SAV subtypes*

241 An approach was designed to map reads from single samples to all six SAV reference genome
242 sequences (note: an SAV6 genome became available while the work was in preparation;
243 (Gallagher et al., 2018). Sequence reads from all eighteen samples mapped exclusively to
244 SAV1, SAV2 and SAV5. Sequence reads generated from two out of five samples collected

from individual fish (common dab) mapped to both SAV1 and SAV5 (Table 2), indicating the presence of viral RNA from two different SAV subtypes in the same host tissue (e.g. Fig. S3). Additionally, eleven out of the thirteen pooled samples contained sequence reads that mapped to two SAV subtypes (Table 2), with both SAV1-SAV2 and SAV1-SAV5 pairings observed. These included pooled samples from both farmed Atlantic salmon and rainbow trout, as well as wild caught Scottish common dab. In all cases, the Sanger-generated sequence confirmed the presence of only the SAV subtype present at higher coverage across a greater proportion of the genome (Table 2).

For all samples showing a co-presence of reads from two SAV subtypes, at least half of the genome was represented; including the majority of the ORF2; sufficient to discriminate between the SAV genotypes (Table 2). A Bayesian phylogenetic analysis of ORF2 was performed, including all the unique publicly available SAV sequences and the consensus sequences assembled during this study; inclusive of SAV subtypes co-present in the same samples (Fig. 2). SAV sequences of co-present subtypes belong to a diverse range of phylogenetic lineages, including distantly related clades for SAV1 and SAV2 (Fig. 2) and were unique compared to the published list of sequenced SAV genes and genomes as well as the list of commonly handled SAV isolates in both Marine Science Scotland and Marine Institute. This abundant novel genetic diversity is incompatible with scenarios where the co-presence of SAV subtypes in the same sample resulted from contamination (see Discussion).

3.3. *Within-subtype SAV diversity*

To test for the existence of within-subtype SAV diversity, we mapped the recovered reads back to consensus sequences for the different SAV genomes. Any samples showing co-presence of two SAV subtypes were mapped to two unique references. Genome-wide single nucleotide variant (SNV) calls were generated for all samples, excluding SNVs with frequencies <5% to

avoid false-positives. All samples showed evidence for minor SNVs with large differences observed between samples (0.01 to 0.77% of genome affected) (Table 3).

Considering the evidence favouring a co-presence of phylogenetically distinct SAV subtypes in single samples, it seemed plausible that distinct subtype strains might also be commonly present in the same sample. However, the short sequencing reads obtained (average fragment length: 192 bp) limits our ability to distinguish such scenarios from viral strains that evolved within-host (Domingo et al., 2012). In an attempt to address this issue, we performed phylogenetic analysis on a short (manually-assembled, see Materials and Methods and Fig. S4) fragment of the SAV E3 and E2 genes for a subset of samples (samples IRE/F3/12, IRE/F38/11, SCO/G415/09, SCO/G572/09, SCO/G573/09, SCO/G582/07) that contained enough variation for reliable viral haplotype phasing (311bp fragment). SAV1 subtype haplotypes identified within each sample were characterised by phylogenetic analysis (Fig. 3). Two distinct SAV1 clades were observed (posterior probability of 0.84), sharing a pairwise nucleotide similarity of 98%, compatible with a co-infection scenario for single-individual samples (IRE/F3/12 and IRE/F38/11) and (at minimum) a co-circulation scenario for the represented pooled samples (SCO/G572/09 and SCO/G415/09). Additionally, isolates IRE/F3/12 and SCO/G572/09 also contained SAV1 haplotypes that branched within monophyletic clades for each sample (e.g. isolate IRE/F3/12 has three SAV1 sequences sharing 99.6% pairwise identity on average). While it cannot be assumed to be the case for SCO/G572/09 (a pooled sample), for isolate IRE/F3/12, these results are consistent with intrahost evolution of SAV.

A broader definition of the SNV landscape of our samples is visualized in Fig. 4 (and Fig. S2), including the proportion of synonymous and non-synonymous variants across different genes in the SAV genome. The caveat to this analysis is that the data represents viral strains from both single fish samples and pools of five individuals. Hence the presence of multiple distinct SAV strains in samples may represent one or multiple of the following scenarios: SAV co-

infection in individual fish, intrahost SAV evolution during the time course of an infection, or, and most likely, the co-circulation of several SAV strains infecting different fish at the farm level. Consequently, this limits the value of statistical analyses to formally contrast differences in SNV rate across different genes and host species, due to confounding effects of possible co-circulations, co-infections and intra-host evolution. Informally, it seems notable that large variation in the number of observed SNVs across samples was inclusive of the different species, with no obvious differences between farmed and wild fish (Table 3). However, we did observe a notably higher number of SNVs in SAV1 compared to SAV2/SAV5 (Table 3), which may reflect a higher natural diversity of this subtype in Scottish and Irish waters. Additionally, we observed that 82% of the SNVs observed were not found in any other sample sequenced in this study (505 unique, 109 shared SNVs) (Fig. S2).

4. Discussion

Second and third generation sequencing platforms have been widely used to study pathogen genomic variation. However, the uptake of such tools to characterize genetic diversity for pathogenic viruses affecting farmed fishes has been slow, leaving knowledge gaps in our understanding of commercially important diseases including PD and SD. The few studies that have achieved a deep profiling of pathogenic viral diversity in farmed fish provide ample evidence for intrahost viral diversity. However, until recently only a few studies considered natural SAV infections, with most work done on cultured viral isolates, which likely lack the natural genetic diversity, instead accumulating novel genetic variation associated with passaging in cell culture (Karlsen et al., 2006). This should be especially true for cultured material consisting of multiple pooled fish, as any genetic variation present will be combined and presumably removed/reduced by selection or drift from the onset of cell culture.

317 In this study, we developed a target enrichment sequencing approach to characterise the genetic
318 diversity of SAV in natural infections and compared the levels of diversity between single-
319 individual and pooled samples. We provide evidence for common co-circulation (and
320 potentially co-infections) of two SAV subtypes and within-subtype strain diversity, both on
321 Atlantic salmon and rainbow trout farms, as well as in wild flatfish populations. Furthermore,
322 SAV1 and SAV5 were co-detected in two single-individual flatfish samples from Dublin Bay
323 representing, to our knowledge, the first empirical evidence for subtype-level SAV co-
324 infection. This finding cannot be explained by contamination, due to the extensive novel
325 phylogenetic diversity of the viral sequences identified with no consensus sequences having
326 100% pairwise identity with any other sequence. Under a scenario of contamination, for
327 example resulting from SAV PCR amplicons previously generated in the lab, we would expect
328 the repeated presence of one or a few contaminating samples. The only isolate used previously
329 in our lab was SAV4640 (accession: JX163854), to which none of the new SAV1 sequences
330 matched. Additionally, several isolates previously identified as SAV1 were found here to
331 contain SAV2 or SAV5; no samples of these subtypes had been subjected to PCR in the
332 laboratory where amplicon libraries were prepared. Finally, under a scenario of contamination,
333 we would expect the issue to impact all samples, given that they were processed together;
334 however, this was not observed, as several contained reads mapping to a single SAV subtype
335 (isolates IRE/F3/12, IRE/F10/12, IRE/F38/11, SCO/G576/07, and SCO/G865/15). This is also
336 seen in Fig. S2, where the majority of SNVs characterised are unique to each sample (~82%)
337 and the frequency of SNVs are not evenly distributed across the samples (minimum of 0,
338 maximum of 126). We thus conclude that the presence of multiple SAV subtypes circulating
339 on single salmonid farms and wild fish populations is a true reflection of natural infections.
340 Importantly, these findings have previously been hidden to consensus sequence approaches
341 reliant on Sanger sequencing of PCR products (Domingo et al., 2012; Hjortaas et al., 2013;

342 Karlsen et al., 2006; Matejusova et al., 2013), advocating a need for routine uptake of higher-
343 resolution sequencing methods from individual rather than pooled samples for epidemiological
344 studies and diagnostics. The high prevalence of within-sample SAV diversity indicates that the
345 dynamics of PD are markedly more complex than widely recognised, suggesting a need for
346 extensive reappraisal and expansion of existing genetic databases to support ongoing disease
347 management decisions.

348 The sequence capture method employed in our study allows for an unbiased characterisation
349 of viral diversity. Our data corroborates previous findings (Hammoumi et al., 2016) that the
350 efficiency of viral sequence capture depends on the initial viral load and is variable between
351 analysed samples. Additionally, the SureSelect^{XT2} protocol used requires pooling of barcoded
352 samples prior to capture; while reducing handling and reagent costs, this prevents the
353 normalization of library quantities between isolates. A difference was also observed in
354 coverage across the SAV genome, which might reflect the natural abundance of the two
355 mRNAs in SAV. In many samples the structural polyprotein, encoded by a ~4kb 3' mRNA,
356 showed higher coverage than the ~8kb 5' mRNA encoding the non-structural polyprotein,
357 which has been observed for other members of the alphavirus genus (Carrasco et al., 2018).

358 While we discovered evidence for within-subtype intrahost variation of SAV in wild fish, our
359 data was unsuitable to phase complete viral genomes for closely related strains. This is due to
360 the use of short-read sequence data, which allows high confidence SNV calling, but makes it
361 challenging to link SNVs separated by distances greater than the sequenced fragment length
362 (192bp average in our study), even when using software dedicated to this problem (data not
363 shown). Hence, future studies of within-subtype SAV diversity will benefit from longer
364 sequence information, which could be generated using the same capture strategy and larger
365 fragment sizes. However, even better results are envisaged by adopting third-generation long-
366 read sequencing tools (e.g. Oxford Nanopore and Pacific Biosciences) (Posada-Cespedes et al.,

2017) and/or linked-read sequencing (Russell et al., 2018), which represent promising tools for ongoing genomic investigations into aquaculture pathogens.

Previous work has characterised the presence of distinct SAV subtypes in proximal geographical locations around Ireland and Scotland (Graham et al., 2012). Interestingly, the industry (https://www.fishfarmingexpert.com/article/msd-survey-vaccination-significantly-reducing-pd-positive-results/) has noted that different SAV subtypes have affected individual Scottish salmon farms in subsequent years, consistent with co-circulation of distinct viral lineages on small spatial scales. Our results are consistent with such non-published reports, as all SAV subtypes detected were previously detected in the same regions (Fig. 1) and demonstrate the presence of multiple SAV strains and subtypes on single farms.

From a practical perspective, it will be important to document the conditions under which complex SAV infections arise, are maintained, and impact pathological outcomes. High-throughput sequencing of pooled samples can accurately identify SAV strains and subtypes present on an individual fish farm; however it does not allow for the characterisation of SAV co-infections and subsequent association between genetic diversity levels (or the presence of individual pathogenic strains) and disease prognosis at the scale of individual fish. Additionally, if Sanger sequencing is used alone for identification of viral genotypes present at the farm level from pooled material, even more information is lost. This is demonstrated by the fact that all Scottish samples tested had the dominant SAV strain correctly genotyped, but missed the secondary strains present in the pooled samples. This is of importance in countries or regions that regulate the salmon industry based on SAV strain presence, such as Norway. Determining the spread and transmission of particularly virulent strains, or even identifying the presence of these virulent strains at low frequencies is challenging, if not impossible using Sanger sequencing approaches. It is now well-established that the implications of co-infections for disease progression can be highly varied, and may range from detrimental to beneficial

(McArdle et al., 2018). In this respect, a priority will be to determine whether higher SAV diversity (either intrahost or co-circulating in a salmon cage) is associated with different disease progression or alteration in mortality rates. Such analyses would be most powerful if done using high coverage genome-wide sequencing of samples from individual fish.

While pooling samples may be appropriate for routine statutory disease surveillance (OIE, 2017), care needs to be taken to ensure that the sensitivity of detection assays is sufficient for detection of viral nucleic acid even when present in lower titres and/or few individuals in the pool (Hall, 2013). Additionally, sampling at the individual level is required for epidemiological studies investigating the origin or relatedness of disease outbreaks where a lack of accurate sequence data can infer incorrect transmission patterns and population dynamics.

Finally, several PD vaccines, with varying efficiencies, are available on the market (Karlsen et al., 2012; Xu et al., 2012). While it is yet to be established whether SAV intrahost variation (or subtype co-circulation on the same farm) impacts the efficacy of PD vaccination, this is an important line of investigation considering previous work, which showed that virulence can vary in multiple-genotype infections compared to single infections (Bose et al., 2016; Lancaster and Pfeiffer, 2012).

In conclusion, we have demonstrated an unbiased approach to enrich viral RNA in infected fish tissues and used it to define previously unrecognized diversity in a viral pathogen responsible for significant commercial losses and welfare issues in salmonid aquaculture. A more thorough definition of the genetic diversity characterising viral infections in aquaculture, especially the associated implications for pathogenicity and disease outcomes, along with a suitable sampling strategy, will be essential in the ongoing battle against viral diseases threatening the expansion of global aquaculture.

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Competing interests

The authors declare no competing interests.

Data Availability

Raw sequence files are available under SRA BioProject PRJNA599596. Genome sequences are provided in Supplementary Materials under Dataset S1.

Figure legends

Figure 1. Geographic distribution of SAV in Scotland and Ireland. Regions previously characterised with the presence of multiple SAV subtypes are indicated with boxes. Pie charts represent isolates characterised in this study with the estimated proportion of co-circulating strains shown by colour.

Figure 2. Bayesian phylogeny showing evidence for two SAV subtypes within single samples used in our study. The tree was built from a 3,935 bp nucleotide alignment of the SAV structural polyprotein (ORF2). The analysis was performed in BEAST2 using the best fit nucleotide substitution model (GTR+G), a relaxed molecular clock model, and a coalescent constant population model. Statistical support for key nodes is indicated by posterior probability values. Consensus sequences from single fish samples have red font titles, while

sequences from pooled fish samples have black font titles. Arrows joining branches indicate subtype-level co-infections within a single fish. Samples with grey font titles were downloaded from NCBI GenBank.

Figure 3. Bayesian phylogenetic analysis of a 311 bp fragment of the SAV E3/E2 genes to identify the relationship of manually-phased haplotypes in six SAV1 samples. Strains are labelled by isolate with letter-based identifiers (e.g. 415a, 415b) indicating multiple strains per isolate. Example co-infections in single-individual samples are indicated by blue arrows, while strains from pooled samples are shown by red arrows. The analysis was performed in BEAST2 using the best-fit nucleotide substitution model (TN93+G), a relaxed clock model and a coalescent constant population tree prior. Statistical support for key nodes is indicated with posterior probability values.

Figure 4. SNV landscape of all samples including secondary strains (n=31) with position of SNV representing genomic location. Synonymous and nonsynonymous SNVs are coloured blue and red respectively. Approximate gene regions are indicted for reference.

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Table 1. Isolate details for the eighteen SAV-infected heart tissues analysed

Sample ID	Year of Isolation	Location of Isolation	Host Species	Source	Sampling Method
IRE/F3/12*	2012	Celtic Sea	Plaice	Wild	Individual
IRE/F6/11*	2011	Dublin Bay	Dab	Wild	Individual
IRE/F7/11*	2011	Dublin Bay	Dab	Wild	Individual
IRE/F10/12*	2012	Celtic Sea	Plaice	Wild	Individual
IRE/F38/11*	2011	Dublin Bay	Dab	Wild	Individual
SCO/G399/09	2009	Argyll	R. trout	Farmed	Pooled (5x)
SCO/G407/09	2009	Shetland	A. salmon	Farmed	Pooled (5x)
SCO/G415/09	2009	Argyll	A. salmon	Farmed	Pooled (5x)
SCO/G424/09	2009	Shetland	A. salmon	Farmed	Pooled (5x)
SCO/G521/10	2010	Shetland	A. salmon	Farmed	Pooled (5x)
SCO/G524/07	2007	Central	R. trout	Farmed	Pooled (5x)
SCO/G572/09	2009	East Coast	Dab	Wild	Pooled (5x)
SCO/G573/09	2009	East Coast	Dab	Wild	Pooled (5x)
SCO/G576/07	2007	South Uist	A. salmon	Farmed	Pooled (5x)
SCO/G582/07	2007	Argyll & Bute	R. trout	Farmed	Pooled (5x)
SCO/G583/10	2010	East Coast	Dab	Wild	Pooled (5x)
SCO/G865/15	2015	Argyll & Bute	A. salmon	Farmed	Pooled (5x)
SCO/G923/15	2015	Shetland	A. salmon	Farmed	Pooled (5x)

*Samples obtained from Marine Institute Ireland are indicated with *, all other samples were obtained from Marine Science Scotland.*

675 **Table 2.** Summary of genome-wide SAV data following sequence capture and Illumina sequencing

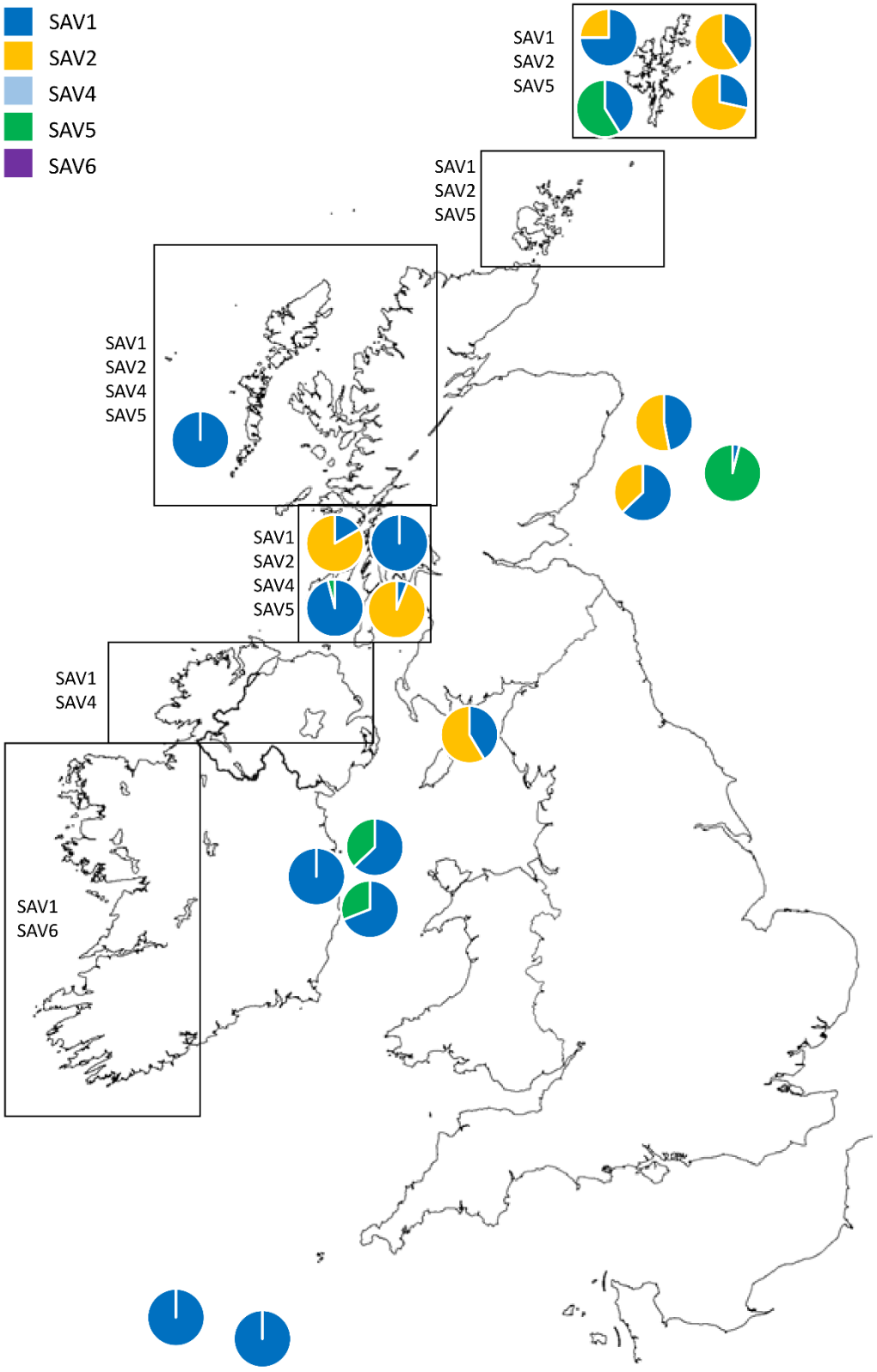
Sample ID	Species	Relative Viral Load (Ct)	Total Reads per Sample	% SAV Reads	% Host Reads	Sanger Subtyped	% SAV1 Genome Covered [mean coverage]	% SAV2 Genome Covered [mean coverage]	% SAV5 Genome Covered [mean coverage]
SCO/G865/15	Atlantic salmon	23.5	39,697,464	91.39	4.63	SAV1	100% [15,126x]		
SCO/G415/09	Atlantic salmon	31.8	9,988,198	45.13	16.22	SAV1	100% [75x]		84% [3x]
SCO/G521/10	Atlantic salmon	34.2	9,548,438	50.65	14.45	SAV1	74% [5x]	46% [3x]	
SCO/G424/09	Atlantic salmon	33.9	9,053,958	17.97	22.80	SAV2	77% [5x]	97% [13x]	
SCO/G407/09	Atlantic salmon	32.2	7,760,266	41.90	32.15	SAV2	100% [27x]	100% [107x]	
SCO/G582/07	Rainbow trout	29.6	5,640,002	9.16	55.24	SAV2	91% [52x]	100% [513x]	
SCO/G399/09	Rainbow trout	31.7	4,657,156	16.87	40.78	SAV2	73% [2x]	100% [191x]	
IRE/F7/11	Common dab	30	167,848	6.40	NA	SAV1	94% [24x]		54% [1x]
IRE/F6/11	Common dab	32.7	209,960	6.60	NA	SAV1	88% [30x]		72% [2x]
IRE/F38/11	Common dab	33.2	3,506,568	19.70	NA	SAV1	96% [422x]		
SCO/G573/09	Common dab	32.9	5,156,948	24.70	NA	SAV2	86% [4x]	100% [18x]	
SCO/G572/09	Common dab	32.4	5,198,444	48.70	NA	SAV2	87% [7x]	98% [15x]	
SCO/G583/10	Common dab	32.7	7,723,112	18.00	NA	SAV5	74% [3x]		100% [47x]
IRE/F3/12	European plaice	32	3,607,684	13.60	NA	SAV1	100% [314x]		
IRE/F10/12	European plaice	23.8	13,304,474	76.90	NA	SAV1	100% [4,864x]		
SCO/G524/07	Rainbow trout	31.1	3,939,136	4.10	28.86	SAV2	58% [40x]	100% [101x]	
SCO/G576/07	Atlantic salmon	31.9	4,404,064	2.90	31.94	SAV1	99% [89x]		
SCO/G923/15	Atlantic salmon	33.9	3,351,272	9.35	43.92	SAV5	47% [1.5x]		54% [5x]

Relative viral load estimated using highly conserved primers in the capsid gene. Only reads with a cut-off q-score of 30 were used. All samples were subtyped using Sanger sequencing for a fragment of the E2 gene. Proportion of reads from the host was not possible for the flatfish species due to a lack of available genomic resources

Table 3. Genome-wide SAV genetic diversity present within SAV subtypes

Sample	Species	Subtype	# SNVs	% Genome Variable	% of SNVs non-synonymous
IRE/F3/12	European plaice	SAV1	78	0.66%	24.36%
IRE/F10/12	European plaice	SAV1	3	0.03%	66.67%
IRE/F38/11	Common dab	SAV1	26	0.22%	38.46%
SCO/G407/09	Atlantic salmon	SAV1	44	0.37%	72.73%
SCO/G415/09	Atlantic salmon	SAV1	46	0.39%	41.30%
SCO/G576/07	Atlantic salmon	SAV1	90	0.76%	73.33%
SCO/G865/15	Atlantic salmon	SAV1	7	0.06%	0.00%
SCO/G399/09	Rainbow trout	SAV2	5	0.04%	60.00%
SCO/G407/09	Atlantic salmon	SAV2	19	0.16%	78.95%
SCO/G424/09	Atlantic salmon	SAV2	4	0.03%	50.00%
SCO/G524/07	Rainbow trout	SAV2	17	0.14%	82.35%
SCO/G572/09	Common dab	SAV2	11	0.09%	72.73%
SCO/G573/09	Common dab	SAV2	5	0.04%	60.00%
SCO/G582/07	Rainbow trout	SAV2	1	0.01%	100.00%
SCO/G583/10	Common dab	SAV5	8	0.07%	87.50%

SNVs called only for consensus SAV sequence for which >95% of total genome length recovered. Only SNVs with frequencies >5% included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SAV2
SAV4
SAV5
SAV6
SAV1
SAV2
SAV5
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SAV2
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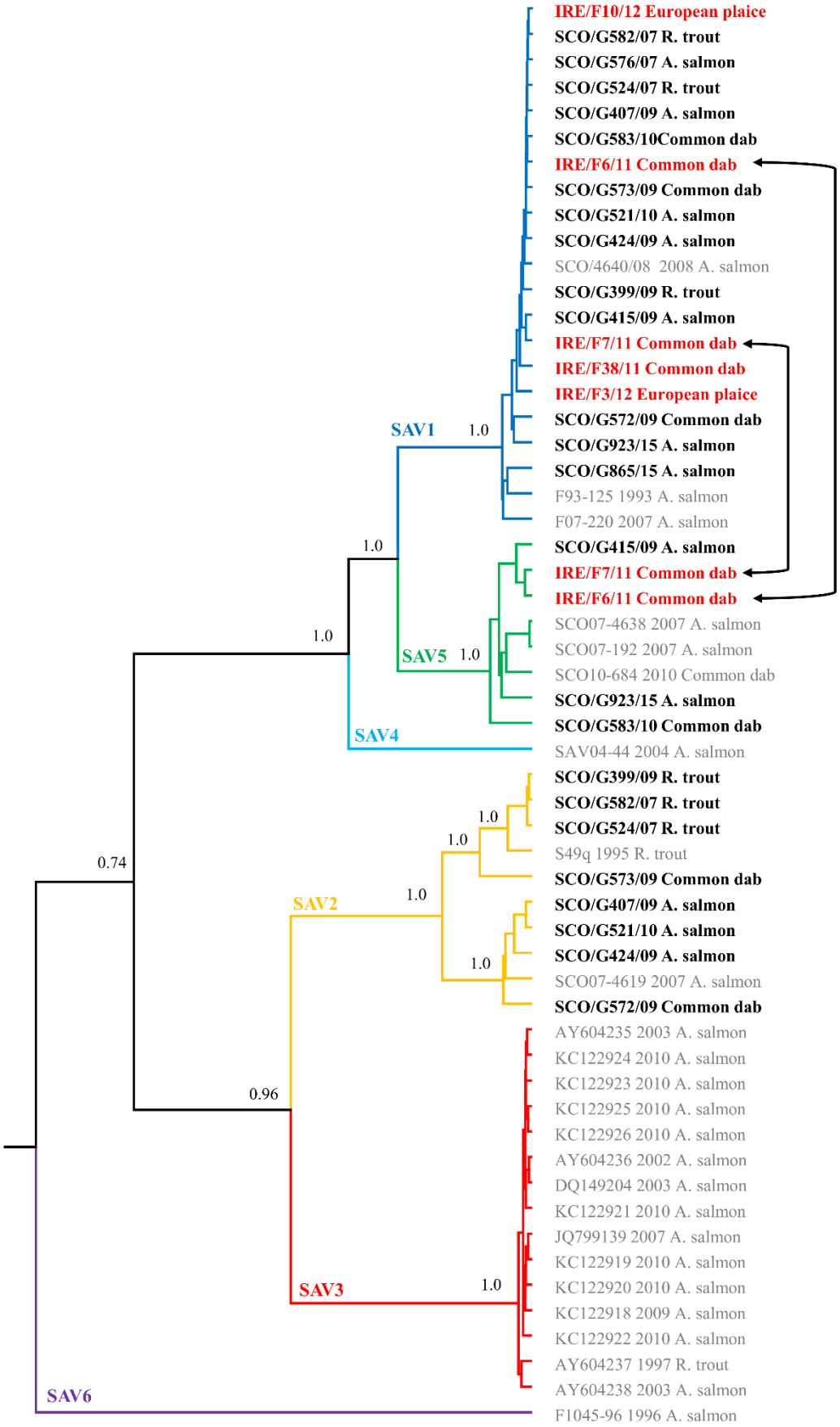
SAV4
SAV1
SAV6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SCO/G582/07 R. trout
SCO/G576/07 A. salmon
SCO/G524/07 R. trout
SCO/G407/09 A. salmon
SCO/G583/10Common dab
IRE/F6/11 Common dab
SCO/G573/09 Common dab
SCO/G521/10 A. salmon
SCO/G424/09 A. salmon
SCO/4640/08 2008 A. salmon
SCO/G399/09 R. trout
SCO/G415/09 A. salmon
IRE/F7/11 Common dab
IRE/F38/11 Common dab
IRE/F3/12 European plaice
SCO/G572/09 Common dab
SCO/G923/15 A. salmon
SCO/G865/15 A. salmon
F93-125 1993 A. salmon
F07-220 2007 A. salmon
SCO/G415/09 A. salmon
IRE/F7/11 Common dab
IRE/F6/11 Common dab
SCO07-4638 2007 A. salmon
SCO07-192 2007 A. salmon
SCO10-684 2010 Common dab
SCO/G923/15 A. salmon
SCO/G583/10 Common dab
SAV04-44 2004 A. salmon
SCO/G399/09 R. trout
SCO/G582/07 R. trout
SCO/G524/07 R. trout
S49q 1995 R. trout
SCO/G573/09 Common dab
SCO/G407/09 A. salmon
SCO/G521/10 A. salmon
SCO/G424/09 A. salmon
SCO07-4619 2007 A. salmon
SCO/G572/09 Common dab
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KC122919 2010 A. salmon
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AY604238 2003 A. salmon
F1045-96 1996 A. salmon
SAV1
SAV5
SAV4
SAV2
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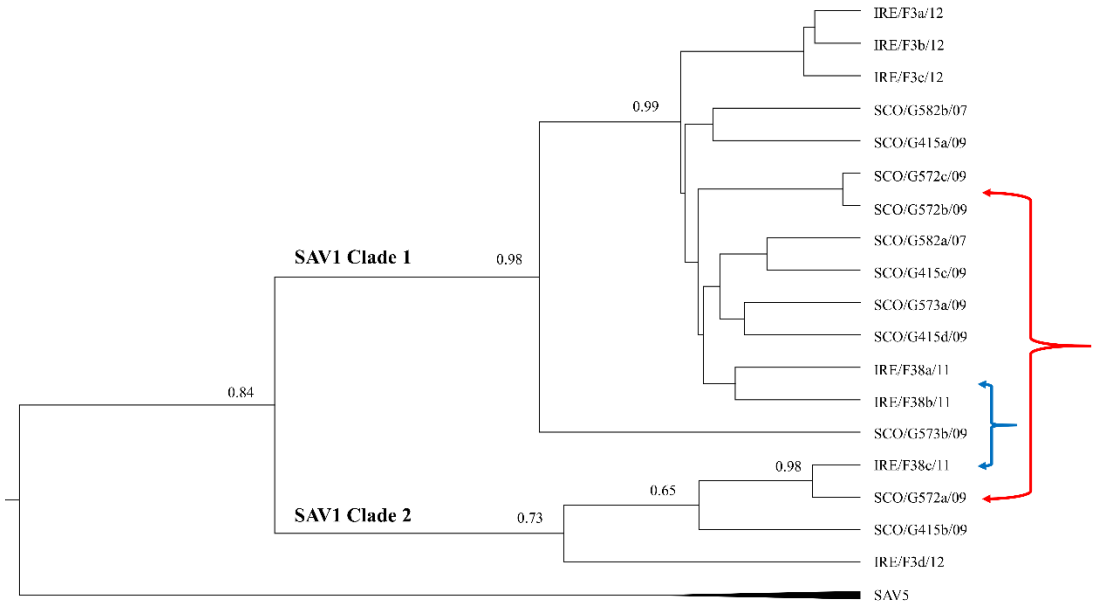
0.96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SCO/G572b/09
SCO/G582a/07
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SCO/G415c/09
SCO/G573a/09
SCO/G415d/09
IRE/F38a/11
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IRE/F38b/11
SCO/G573b/09
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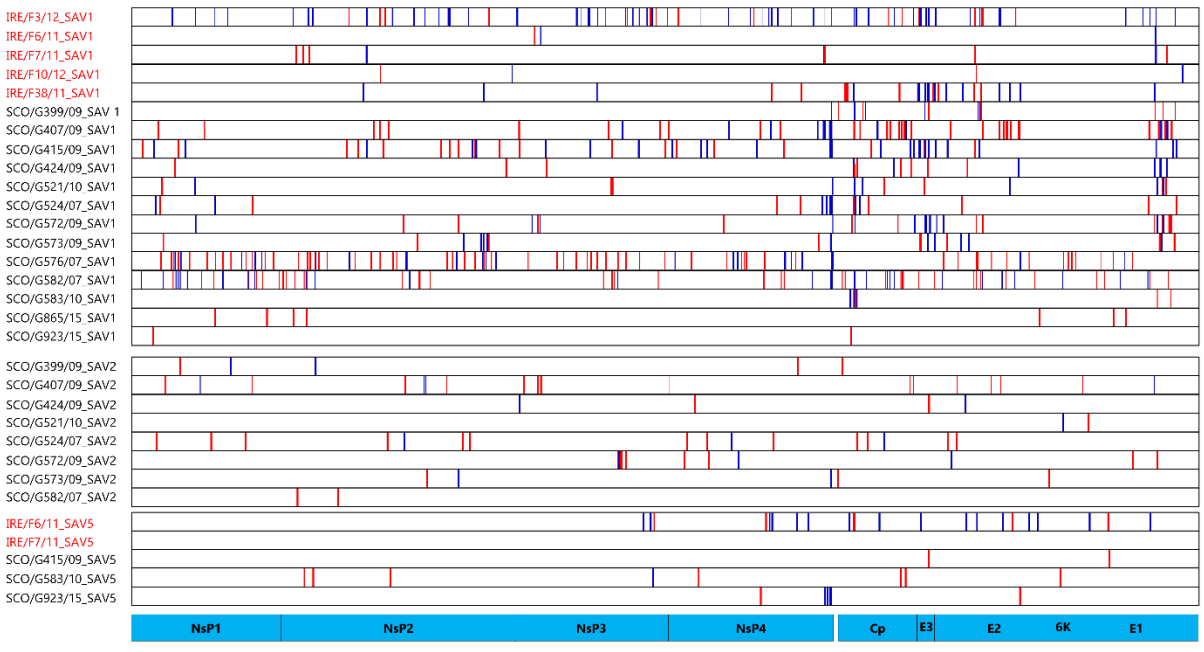
SCO/G415b/09
IRE/F3d/12
SAV5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IRE/F7/11_SAV1
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NsP1
NsP2
NsP3
NsP4
Cp
E3
E2
6K
E1

SUPPLEMENTARY MATERIAL

Genome-wide target enriched viral sequencing reveals extensive 'hidden' salmonid alphavirus diversity in farmed and wild fish populations

Michael D. Gallagher, Iveta Matejusova, Neil M. Ruane, Daniel J. Macqueen

Contains:

Fig. S1, S2, S3, S4

Dataset S1.

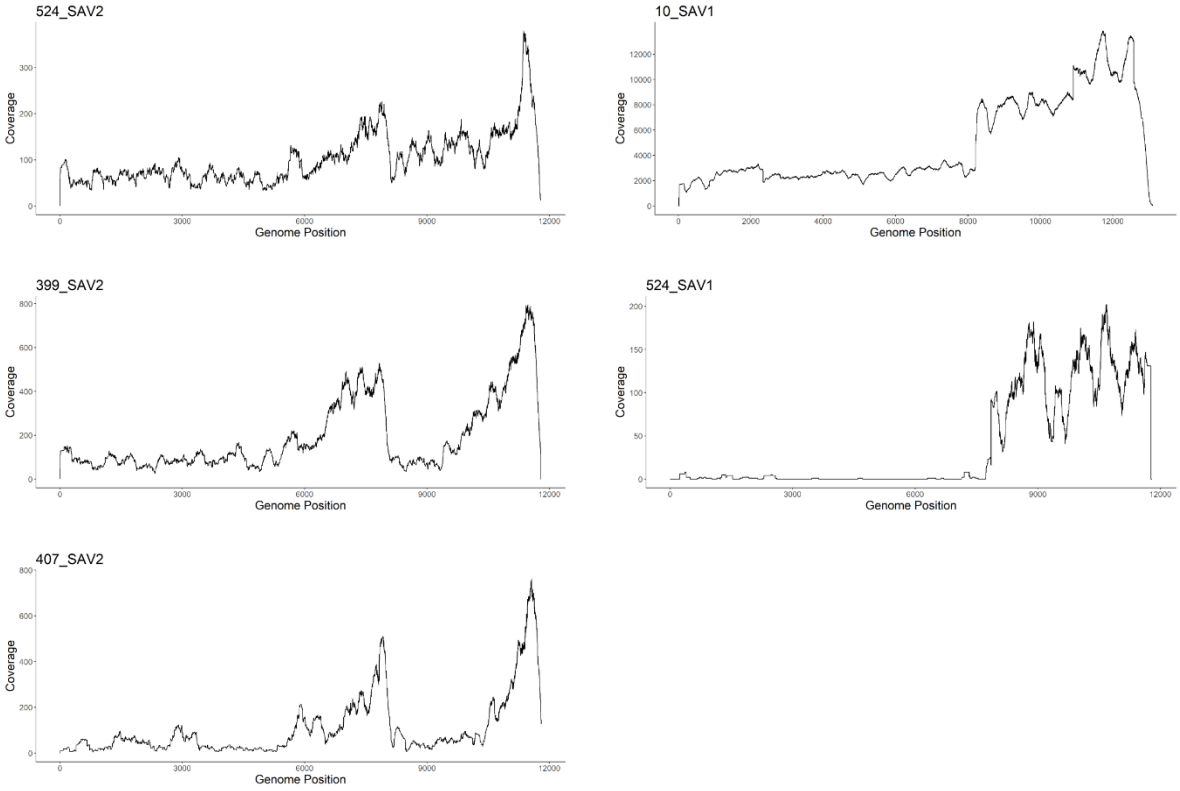

Fig. S1. Coverage plots of representative isolates showing an increase in coverage over the structural polyprotein for SAV1 samples, but an increase at the 3' end of each polyprotein in the SAV2 samples.

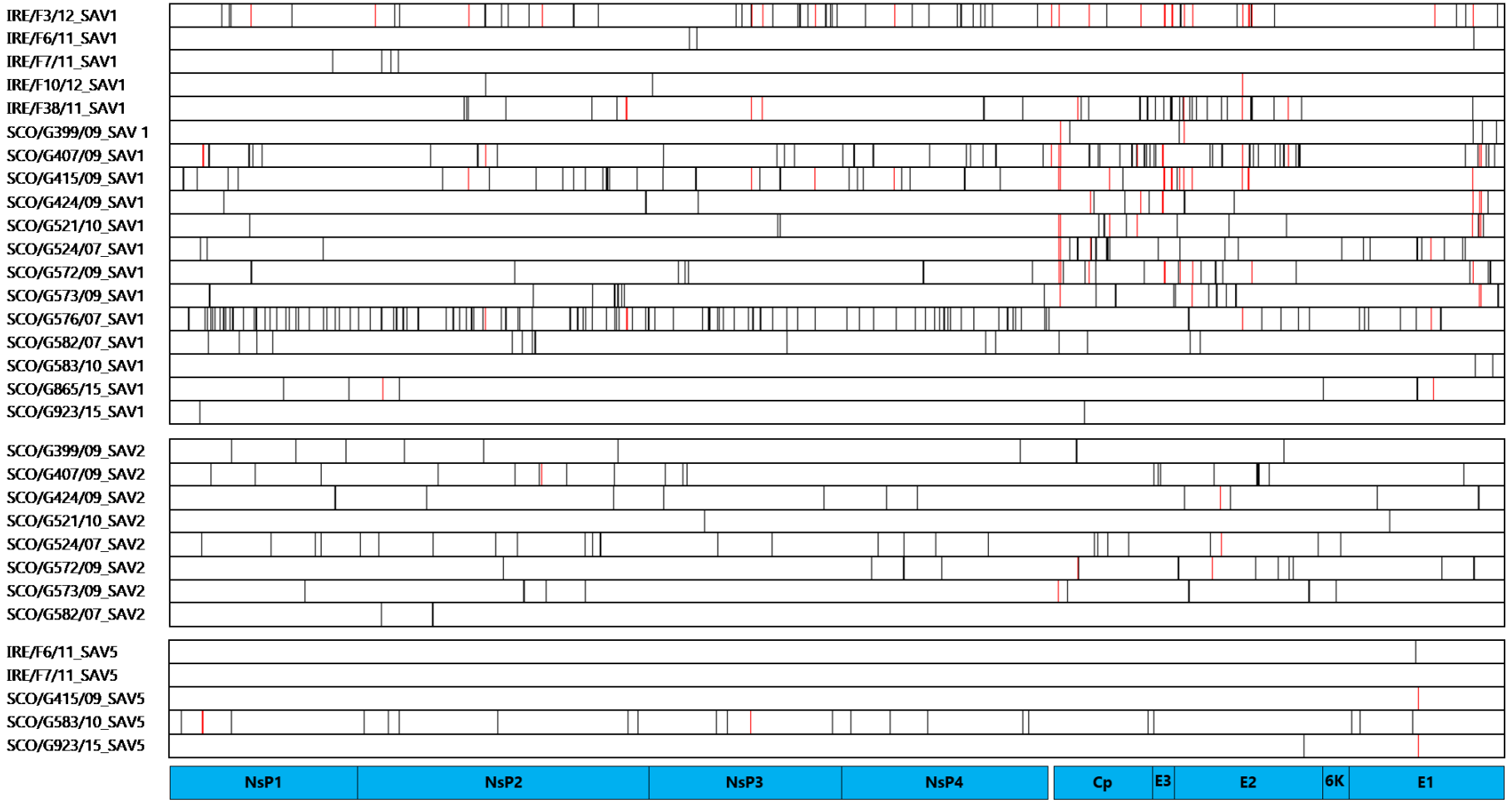

Fig. S2. SNV landscape of all samples including secondary strains (n=31) with position of SNV representing genomic location. SNVs are coloured by identity to other variants identified in this study. Variants coloured black are novel and unique to that sample, red variants represent SNVs found in other samples. Approximate gene regions are indicted for reference.

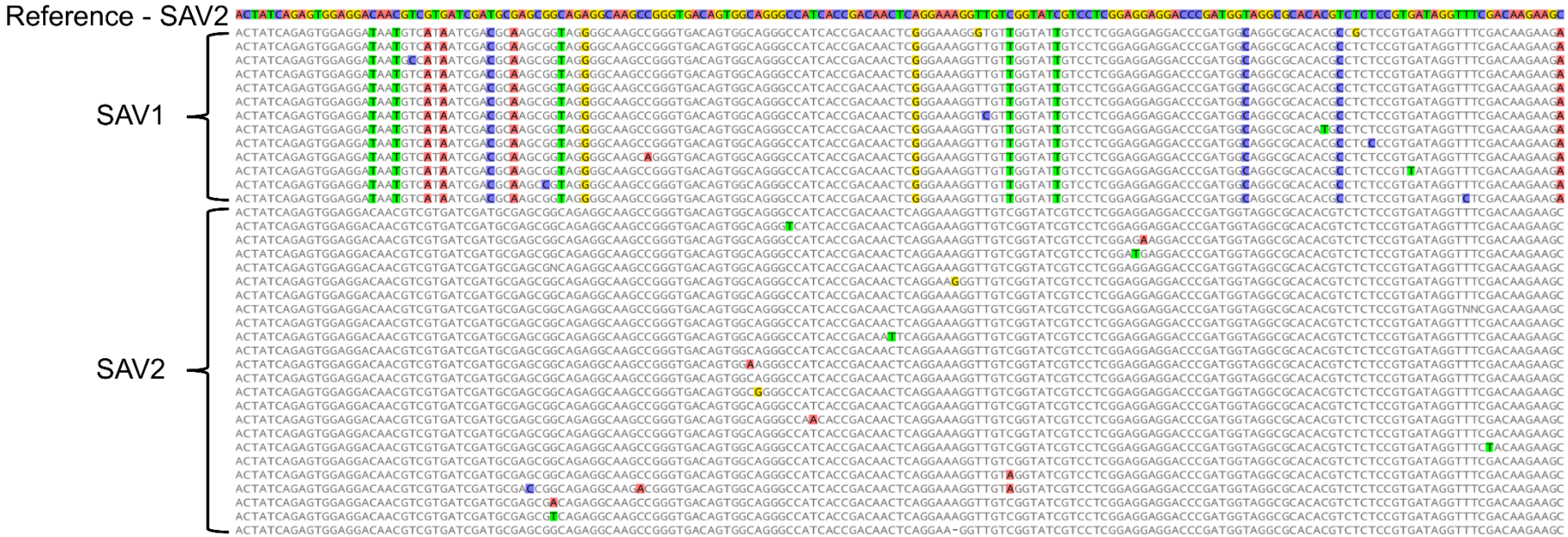

Fig. S3. Visualisation of a subtype-level ‘co-infection’ in a pooled sample where reads from SAV1 clearly distinguishable from those of SAV2.

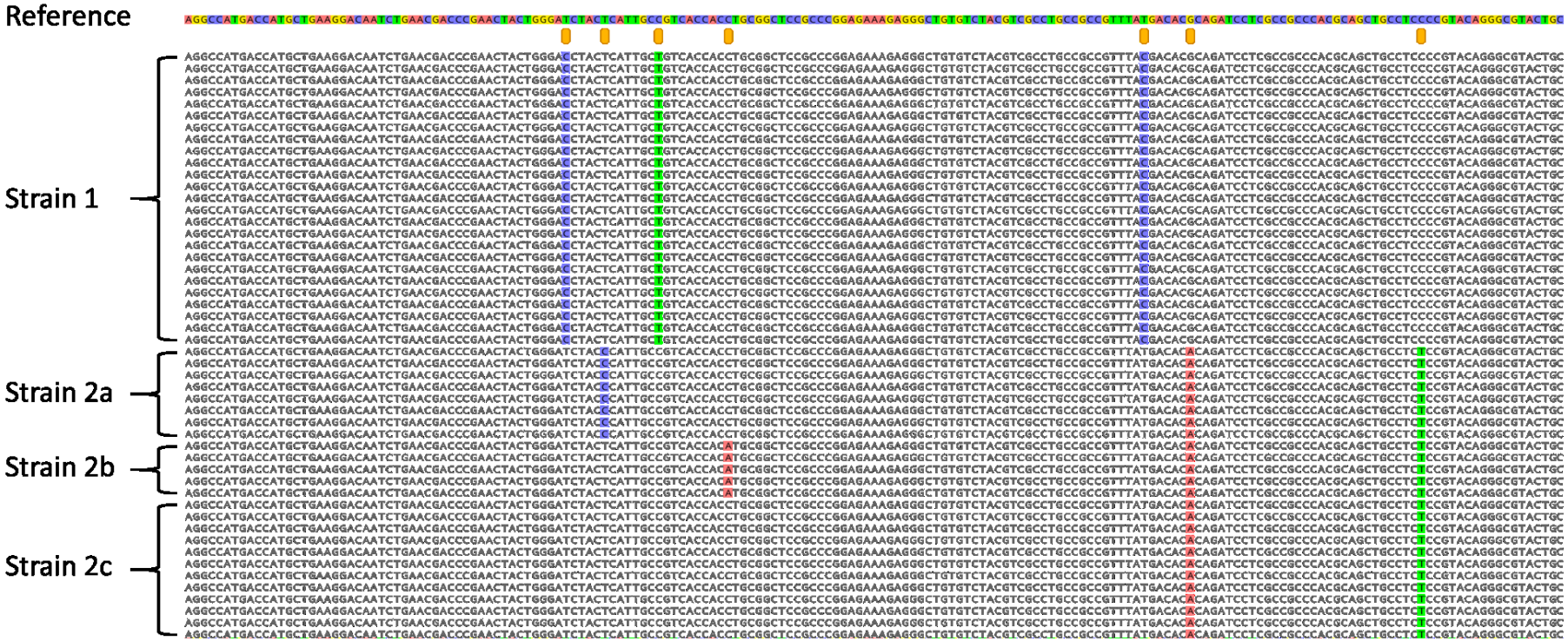

Fig. S4. Visualisation of haplotype-level reconstruction of the viral population within an infected sample. Haplotypes 2a, 2b and 2c are all more closely related to each other than they are to haplotype 1, indicating the presence of a coinfection of two viral strains (strain 1 and strain 2) and the subsequent intra-host diversification of one of these stains (strain 2)

Dataset S1. Genomic sequences of the dominant and minor subtypes in each isolate. Sequences are labelled in the following format:

'Dominance'_'CountryofOrigin'/'IsolateNumber"/'YearofIsolation'_'Subtype'

>Minor_IRE/F6/11_SAV5

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>Minor_IRE/F7/11_SAV5

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